THE ECOLOGY OF SUBSOCIALITY IN *Theridion pictum* (WALCKENAER), (ARANEAE:THERIDIIDAE).

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ABSTRACT

Theridion pictum , is a common but little studied species of comb-footed spider. Hence, the first part of this thesis documents aspects of its' lifecycle and behavior. I present information on the spatial and temporal patterns of egglaying and hatching, methods of prey capture, and types of maternal care. The remainder of the thesis examines the effects of food availability on the behavior of spiderlings. Experimental manipulations indicate that in those webs where less food was provided, spiderlings dispersed significantly earlier and in significantly greater numbers than spiderlings from webs where abundant food was provided. Similar patterns are observed in undisturbed webs. Food availability also affects the pattern of sex-biased philopatry and dispersal. Although both sexes are more likely to remain at the maternal web when more food is available, females are relatively more likely to do so. Similarly, when less food is available, females are relatively more likely to disperse than males. Thus, females dispersal patterns appear to be very sensitive to food availability while males may be responding to female availability. I argue that these results demonstrate the importance of food availability as a permissive factor in the evolution of social spiders from subsocial ancestors.

Should I stay or should I go?

If I stay it will be trouble.

If I go it will be double.

- *The Clash*, 1982

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INTRODUCTION

Theridion pictum is a subsocial spider. That is, the mother takes care of her offspring for an extended period of time after they hatch. This is in contrast to many species of spider which simply lay an egg case and leave it, or at best, guard the sac only until the young hatch. I originally became interested in understanding what features of the environment were important in the evolution of subsociality. Typically, behavioral ecologists focus on four interrelated factors in their efforts to understand the causes of a particular social system. These are prey distribution, predation and/or parasite pressure, the distribution of structural habitat features and phylogentic constraints (in the case of spiders primarily web type and lifecycle). My emphasis is primarily on food distribution. In particular, I have examined how food availability affects the duration of parental care.

In chapter one, I will present information on the biology of *T. pictum.* While certain aspects of this species biology are typical of the genus and hence are part of common knowledge, no detailed studies of this particular species have previously been published. I present both general information about the lifecycle of *T. pictum,* which is needed to understand my experimental work, and more detailed information about parental care and dispersal. The latter includes data on fecundity, types of parental care that are provided and effects of food availability on the rates of dispersal and growth. I also indirectly examine the effect of parental care on the reproductive success of females. The length of time that a mother is absent is found to affect the number but not the average size of spiderlings remaining in the web.

In chapter two, I present the results of experiments on the relation between food availability and parental care. I show that the dispersal behavior of spiderlings of this species is affected by the availability of food in the maternal web. Experimental

manipulations indicate that in those webs where less food was provided, spiderlings dispersed significantly earlier and in significantly greater numbers. I also examine the differing sensitivities of males and females to food availability. Females are relatively more likely than males to remain in the maternal web when more food is available but are more likely to disperse when less food is available. However, male growth rates exceed that of females when in a food rich environment. These results are discussed in terms of the differing strategies of males and females for increasing lifetime reproductive success.

In chapter three, I discuss these results in the context of the evolution of subsociality and of the evolution of social spiders from subsocial ancestors. I argue that my experimental results illustrate the importance of food availability as a permissive factor in the evolution of social spiders from subsocial ancestors. I also argue that *T. pictum* is in many ways preadapted to evolve subsociality. I believe that above all, the ability of *T. pictum* to safely capture large and numerous prey allows the mother to provide enough food for her offspring to remain in the safety of her web, without them suffering from high rates of cannibalism.

Chapter One

NATURAL HISTORY OF *Theridion pictum.*

INTRODUCTION

As with many common spiders, species of the genus *Theridion* (Araneae: Theridiidae) have been the frequent subject of observational studies during the last century (Comstock 1912, Lockett 1926, Nielson 1932 in Nørgaard 1956), but of very few experimental or ecological studies. The most notable exceptions are Nørgaard's detailed study of *Theridion saxatile* (C.L. Koch), a subsocial European Theridiid (1956), and Kullman's work with a variety of subsocial Theridiids (1972). However, the behavioral ecology of many subsocial spiders is beginning to receive greater attention (Ito 1985, Krafft et al. 1986). While this partly results from an increasing number of spider studies overall, it is especially related to the large and growing interest in cooperatively social spiders (Aviles 1987, Roeloffs and Riechert 1988, Vollrath 1986, to name a few of the most recent studies). One important method for gaining insight on the causes of grouping in the cooperatively social spiders is by studying the behavior and ecology of related, but subsocial species. Furthermore, there is circumstantial evidence that the cooperatively social spiders have evolved from subsocial ancestors (Buskirk 1981, Kullman 1972, Shear 1970 and see chapter three). For this reason, subsocial *Theridion* species are especially interesting; they belong to the same family as the cooperatively social, neotropical spider, *Anelosimus eximius* (Keyserling).

Prior to my research, the only available experimental study of *Theridion pictum* (Walkenaer) was an unpublished report of a class project led by Dr. Ruth Buskirk at the University of Minnesota Forestry and Biological Station during the summer of 1983. In this chapter, I present new information on the natural history of *T. pictum*.

This includes observations on the general natural history, more specific data on spatial and temporal patterns of egglaying and hatching, and finally, I examine the effect of maternal care upon spiderling growth and persistence at the maternal web.

METHODS

All research was conducted at the University of Minnesota Forestry and Biological Station in the Lake Itasca State Park, Minnesota, during the months of June through September 1986, and April through September 1987. To avoid complications due to differing habitat structure, I studied webs primarily on white spruce trees, *Picea glauca* . For practical reasons, I only studied webs that were higher off the ground than my knees but lower than my head, (18" to 63").

In mid-June of 1986, I marked the location of 108 webs with small, numbered pieces of flagging tied to nearby branches. These webs were spatially divided into three groups, those that were; ≈20-30 meters from the lake, ≈55-70 meters from the lake, and ≈170-250 meters from the lake. I censused each web nearly every day from June 16 to August 29. This involved recording whether an adult female was present, whether any egg sacs had been laid or hatched, and estimating the number of spiderlings present. I also used a censusing technique to obtain information about feeding behavior. In a series of bouts each lasting five or more hours, I observed each web once an hour and recorded whether any of the inhabitants of a web were feeding. A relative index of feeding was constructed by simply dividing the total number of hours that a web had feeding inhabitants by the total number of hours observed. This index will be referred to as the 'feeding frequency index' to distinguish it from the 'summed prey index' as

described below.

In addition, twenty-nine unmarked webs were collected and their contents analyzed. Spiderlings were counted and the length of their bodies measured. Egg sacs were dissected open and the number of eggs counted. Retreats were also dissected and the carcasses in them were measured. The food availability of each web could then be characterized by the summed length of prey items found in the retreat. This index is referred to as the 'summed prey index'. It was used strictly for collected webs while the 'feeding frequency index' was used for webs that were still intact.

In mid-June of 1987, 179 webs were marked. These webs were distributed in six different areas. As in 1986, the webs were arranged in three areas ranging in distance from the lake (adjacent: <5m, Mid: 40-50m, Far: 170-250m), however, each of these areas were then divided into two; a sunny area and a shady area. Webs were monitored for the presence or absence of an adult female, the number of egg sacs and whether the first egg sac had hatched. The number of spiderlings present in each web was not counted in 1987. However, the webs were more closely monitored for parasites and the presence of other species of spiders or their egg sacs. Full censuses, (every web), took place nearly every day from June 14 to July 9, and then only once a week until August 6. Partial censuses were conducted daily from July 10 until July 22.

In 1987, the webs were randomly assigned numbers at the beginning of the season. Once a week, the six remaining webs that had the lowest numbers while also having an adult female and/or offspring present, were collected. This procedure continued from June 29 to August 3. Webs were collected whole and then dissected in the laboratory. All spiders were removed and preserved in 75% isopropyl alcohol. The length of the first

tibia plus patella was measured on each spiderling. When possible, the egg sacs were also removed from the web and the empty egg shells were counted. Additional unmarked webs were also collected for the purpose of counting the number of eggs per sac.

Insects were identified using Borror and White (1970). Identifications of *T. pictum* voucher specimens were made by Dr. Herbert Levi and were placed in the collection of the Harvard Museum of Comparative Zoology. Additional identifications of spiders were possible using Levi (1957) and Kaston (1953).

RESULTS AND DISCUSSION

General information

The web of *T. pictum* is a roughly pyramid shaped, tangle web with a retreat built at the apex, just under a branch (see Figure 1.1). This retreat is built from pine needles and carcass remnants, sewn together with silk. The mature female usually builds only one web which she inhabits for the duration of the season. This contrasts with the behavior of many orb and sheet-web weavers (primarily Araneidae and Linyphiidae) that change web sites frequently throughout the season (Janetos 1986, D.A. Hanych pers. comm.).

T. pictum individuals overwinter as subadults and emerge in early spring, (April to May in Minnesota). By mid June most individuals have matured and mated, however, I have observed one mating as late as July. After this period, males can no longer be found. Egglaying and hatching occurs during the beginning of the summer, (June/July).

Egglaying and hatching

The egg sac of *T. pictum* is tan and round, the result of the mass of eggs being

heavily wrapped by silk. In size, it is nearly as large and as heavy as the female. Each sac contains a mean of 67.3 eggs (n=26, range=28 to 111). Until the spiderlings emerge, the female attends to her egg sac by storing it tightly in the retreat at night and on rainy days, and by taking it out into the web during the day. While it has been proposed for other *Theridion* species that bringing the sac out of the retreat results in it being warmed by the sun and presumably speeding up development (Nielson 1932), Norgaard (1956) effectively demonstrated just the opposite. Using thermocouples to measure air temperature inside and outside the retreat of *T. saxatile*, he found that average daytime temperatures inside the retreat were 10^{o} to 14^{o} C higher than the surrounding air temperature. Presumably, the nest also retains some of this heat at night. He also found that eggs and first instar spiderlings die at temperatures above 39^{o}C, a common daytime temperature inside the retreat. Furthermore, he observed that females carry the egg sac inside the retreat when the air temperature drops below 30^{o}C and remove it from the retreat when the temperature inside reaches 35.7^{o}C. Thus, the female seems to use the retreat as an incubator but must remove the egg sacs when it gets too hot. This behavior is also common to *T. pictum* and presumably functions in a similar manner.

While the female usually lays her first egg sac in June, the mean date can differ significantly from year to year. In 1986, the mean date of egg laying was June 27, while in 1987 the mean date was June 19, (Mann-Whitney $U=175.5$, $N_1=45$ $N_2=42$, $P<.0001$) (see Table 1.1). Between the time when the egg sac is laid and when the spiderlings actually emerge from the sac, the 'incubation time', spiderlings hatch from their individual eggs and undergo one molt; thus they emerge from the sac as second

instar spiderlings. The 'incubation time' also varies from year to year, but not significantly. In 1986, the mean 'incubation' time was 14.0 days, while in 1987, it was 15.3 days (Mann-Whitney U=401, N_1=32 N_2=28, P<.31), (Table 1.1). However, as with egglaying, the mean date for the hatching of the first egg sac does differ significantly from year to year. In 1986, the mean date was July 11 while in 1987 the mean date was June 29, (Mann-Whitney U=423.5, N_1=56 N_2=110, P<.001), (table 1.1). Some of this variation in egglaying dates may be due to yearly weather variation. For example, in April and May of 1986, the calculated 'departure from normal' temperatures were +4.5 and +2.2 (^{o}F), respectively (Climatological Data, Minnesota 1986). In 1987, when spiderlings hatched *earlier*, the calculated 'departure from normal' temperatures were +10.0 and +5.0 (^{o}F), respectively (Climatological Data, Minnesota 1987). This suggests that warmer spring temperatures accelerate the lifecycle. This may be because juveniles emerge from hibernation earlier, more food is available earlier, or maturation, mating and egglaying all occur more swiftly with warmer temperatures. Probably a combination of all three factors is important.

Frequently the female lays her second egg sac frequently within one day of the emergence of spiderlings from the first egg sac. While there is no significant difference in the number of eggs laid in the first and second egg sac, the actual numbers of spiderlings which survive to the first molt does differ. From the first egg sac, 92.2% of the eggs hatch and 79.1% molt (N=17). Yet, of the 87.4% of the eggs in the second sac that actually hatch, only 7.5% reach the first molt (N=17). Siblicide by older spiderlings is suspected to be the major cause of pre-emergence mortality for second

sac spiderlings. However, these results may have been affected by the artificial caged situation, (see chapter two).

There is also variation in the time of egg laying and of hatching between *locations*. In 1986, I found that spiders living in the area furthest from the lake laid their first egg sacs 10 days later than spiders living close to the lake, (Mann-Whitney U = 36, N_1= 9 N_2=29, P<.005). In 1987, in an attempt to elucidate the reasons for this variation, I marked webs in three areas again varying in distance from the lakeshore. Each of these was in turn split into two areas with higher and lower shade/tree density. I chose to examine the effect of shade in addition to distance from the lake in 1987 since I suspected that temperature during incubation directly affects hatching date and/or food availability prior to egglaying indirectly affects hatching date. I found that spiderlings emerged from the first egg sacs significantly earlier in the sunny areas than in the shadier areas, (Mann-Whitney U=956, N_1=43 N_2=65, P<.01), (see Table1.2). This provides some support for my prediction that hatching would occur earlier in warmer areas. However, in contrast to the previous year, spiderlings in the webs that were of intermediate distance from the lake hatched significantly earlier than those in the areas nearest and furthest from the lake, (Kruskall-Wallis H=29.194, d.f=2, n=108, P<.005). Thus, being close to the lakefront, a source of emerging insects, does not in itself lead to earlier hatching dates. There are two explanations for this. One, food availability prior to egglaying does not affect hatching date, or, the effect of proximity to the lake is moderated by other factors such as temperature or shelter from storms.

Feeding habits

T. pictum captures a wide variety of prey, ranging from tiny psyllids (Homoptera, measuring 2-5mm, Borror and White 1970), up to larger damselflies and the occasional dragonfly (Odonata). The most common items are intermediate sized Diptera, Ephemeroptera, and Trichoptera. Prey capture is accomplished by drawing silk from the spinnerets using special combs located on the tarsi of the last pair of legs. The spider uses these combs to rapidly throw silk over the prey. As the preys' movements become subdued, the spider briefly closes in and bites the prey. These two steps may be repeated several times until the prey is subdued completely. The spider then cuts all but a few of the threads holding the carcass in the web, and draws the carcass up with these threads, repeating the process as necessary until the carcass is in or near the retreat. Only then does she feed upon it.

Parental care

Many *Theridion* species are subsocial to some degree. Hirshberg (1969, in Toft 1978) describes a gradient of sociality that can be used to classify the degree of subsociality in *Theridion*. Class I species are solitary, i.e. not subsocial. In class II species, the mother provides the offspring with prey for a limited amount of time after their emergence. Finally, class III species feed the very young spiderlings by regurgitation, medium age spiderlings are provided with prey and older spiderlings are observed to cooperate in capturing prey. I would classify *T. pictum* as belonging to this third group. Although I have never observed regurgitation, the remaining behaviors which characterize the third level of subsociality are observed in *T. pictum*. Certainly, the mother actively provisions the young with food. At first, she drags the prey to the retreat where the spiderlings are passively waiting to feed. Later, as the spiderlings

become more active, they may meet the mother halfway. Eventually, they will even assist her or each other to capture the prey, although it is dubious whether their assistance is always effective.

Unlike many Araneids or Linyphiids, the spiderlings do not disperse *en masse*. My own observations indicate that individual spiderlings gradually begin to spend more time waiting at the periphery of the web and catching very small prey on their own, only cooperating with others in the capture of very large prey. I suspect this phase immediately precedes an active dispersal phase. Most Theridiids are believed to disperse by ballooning (Bristowe 1939). However, I have not been able directly or indirectly to observe this, although I may have looked at the wrong time of the year.

Frequently, the mother disappears or dies in the web prior to the dispersal of all the spiderlings. Females probably die or disappear for many different reasons. I have occasionally observed that her body is eaten by the offspring. Disappearance may also be due to starvation, predation, or parasitism; problems common to many different groups of animals. In addition, these spiders are frequently evicted from their retreats and webs by larger spider species and are also vulnerable to drowning and web destruction by rain. I have found there is a significant positive correlation between the amount of rainfall and the number of webs which disappear on that day, (Spearman's Rank Correlation Coefficient=.358, N=59, P<.01), (data are for 1986, see Figure 1.2). Available information on the causes of disappearance of the mother have been summarized in Table 1.3. After the mothers' disappearance, or possibly just as they grow larger and become food limited, aggression levels between the siblings appears to increase and it is common to observe smaller spiderlings being displaced from feeding

sites by larger spiderlings.

The length of time that spiderlings persist in the maternal web differs from web to web and from year to year, however, it is very difficult to accurately measure dispersal in a natural setting. Furthermore, because spiderlings do not disperse as a group, there is no single dispersal time. In Table 1.4, I have presented three different measures of dispersal time; the number of days from hatching until fewer than ten or fewer than two spiderlings remain and the number of spiderlings remaining on August first. I have also included the results of the same measurements upon caged spiders, (chapter two). In addition, Figure 1.3 graphically illustrates the overall time course of dispersal in 1986. The length of time that spiderlings remain in the web appears to be affected by the amount of food available. I have found a significant positive correlation between the 'feeding frequency index' and the time until fewer than 10 spiderlings remained in the web in 1986, (Spearman's rank correlation coefficient=.384, N=56, P<.01), (Figure 1.4). Recall that the 'feeding frequency index' is the number of hours that a web was observed to have feeding individuals divided by the total number of hours observed, (see methods).

The rate at which spiderlings grow can also be greatly affected by food availability. There is a significant positive correlation between the 'summed prey index' and both the mean body *length* of spiderlings from webs collected in 1986 (Spearman's rank correlation coefficient=.407, N=27, P< .05). and the *number* of spiderlings in the web, (Spearman's rank correlation coefficient=.697, N=27, P<.01), (Figure 1.5, a and b). Recall that the 'summed prey index' is the sum of the length of prey items found in the retreat after collection of the web, (see methods). This same relationship holds

for spiderlings reared in cages. At the end of the experiment, (described in chapter two) spiderlings that remained in webs which were provided with abundant food were significantly larger than those from cages that were provided a limited amount of food, (Mann-Whitney $U=910.0$, $N_1=17$, $N_2=180$, $P<.01$).

These findings provide strong support for the idea that growth rates are very flexible in this species and that increased levels of food availability permit spiderlings to tolerate each others presence since spiderlings are both larger *and* more numerous in webs with the higher 'summed prey index'. The implications of these findings for our understanding of the evolution of sociality will be discussed further in the next chapters. An interesting aside, however, is that there is no significant size difference in spiderlings that *dispersed* from high and low food treated cages in the experiment that is described in chapter two.

I have attempted to examine, indirectly, whether providing parental care actually increases the females' reproductive success by comparing the average size, and/or number, of spiderlings collected from 17 webs with, and 15 webs without adult females present. Assuming that maternal care is valuable to spiderlings, I had predicted that the mean size of spiderlings would be greater in webs having adult females. I also predicted that greater numbers of spiderlings would be found in webs with an adult female present. Presumably, more food is available to the spiderlings when the mother is present.

The simple presence or absence of the mother did not explain any difference in size or number. A more accurate measure of maternal presence, number of days the mother has been gone, (mother present = 0 days), does explain a significant amount of the

variance in the mean numbers of spiderlings (Linear regression, F=4.807, d.f.=20, P<.05), the longer she has been gone the fewer spiderlings remain. Yet, the number of days gone is not a good predictor of the mean size of spiderlings at a web, (Linear regression, F=.253, d.f.=20, P=.62). However, neither of these is significant when a Spearmans' Rank Correlation is used instead of a linear regression.

At first it may seem surprising that the number of days the mother has been gone explains no difference in the mean size of spiderlings. A better understanding of size specific dispersal patterns may clarify the results. Assuming that growth rates are dependent on the amount of available food, and also assuming that more food is available in webs with the mother present (see below) then, if individuals disperse *randomly* with respect to size there should be a difference in average size of spiderlings from webs with and without mothers. On the other hand, if the largest individuals disperse first, (this might be likely if they become food limited more quickly and presumably can disperse more safely), then the discrepancy in sizes should be even greater. This is because webs with mothers present should have larger spiderlings that do not disperse, while webs without mothers should have smaller spiderlings and the largest of these will have dispersed. A third alternative is that the smallest spiderlings disperse first. Then, there may not be a size difference dependent on the length of time the mother has been absent. There may be two reasons for this. First, the longer she has been gone the more small spiderlings have dispersed and second, a few spiderlings may be eating the smaller ones and thus not actually be food limited. These two factors could push up the average size of spiderlings from webs without mothers, resulting in no significant difference. Observations support this hypothesis since small spiderlings are often

displaced from feeding sites by larger spiderlings. In other words, it is actually the smallest spiderlings that become food limited first and are presumably also more vulnerable to siblicide. Technical considerations would also increase the difficulty of detecting any effect on mean size. That is, my measurements were of mean *leg* length which may change more slowly than body length. Leg length remains constant between molts while body size may vary.

Conclusion

In this chapter I hope to have provided the reader with a better understanding of the biology of the spider, *Theridion pictum* in preparation for understanding my experimental work. I have presented new data regarding the temporal and spatial patterns of egglaying and hatching. In particular, I have attempted to examine how weather, distance from a food source, and sunlight all affect hatching times. I have also examined the effect of maternal care on the persistence and growth rates of spiderlings.

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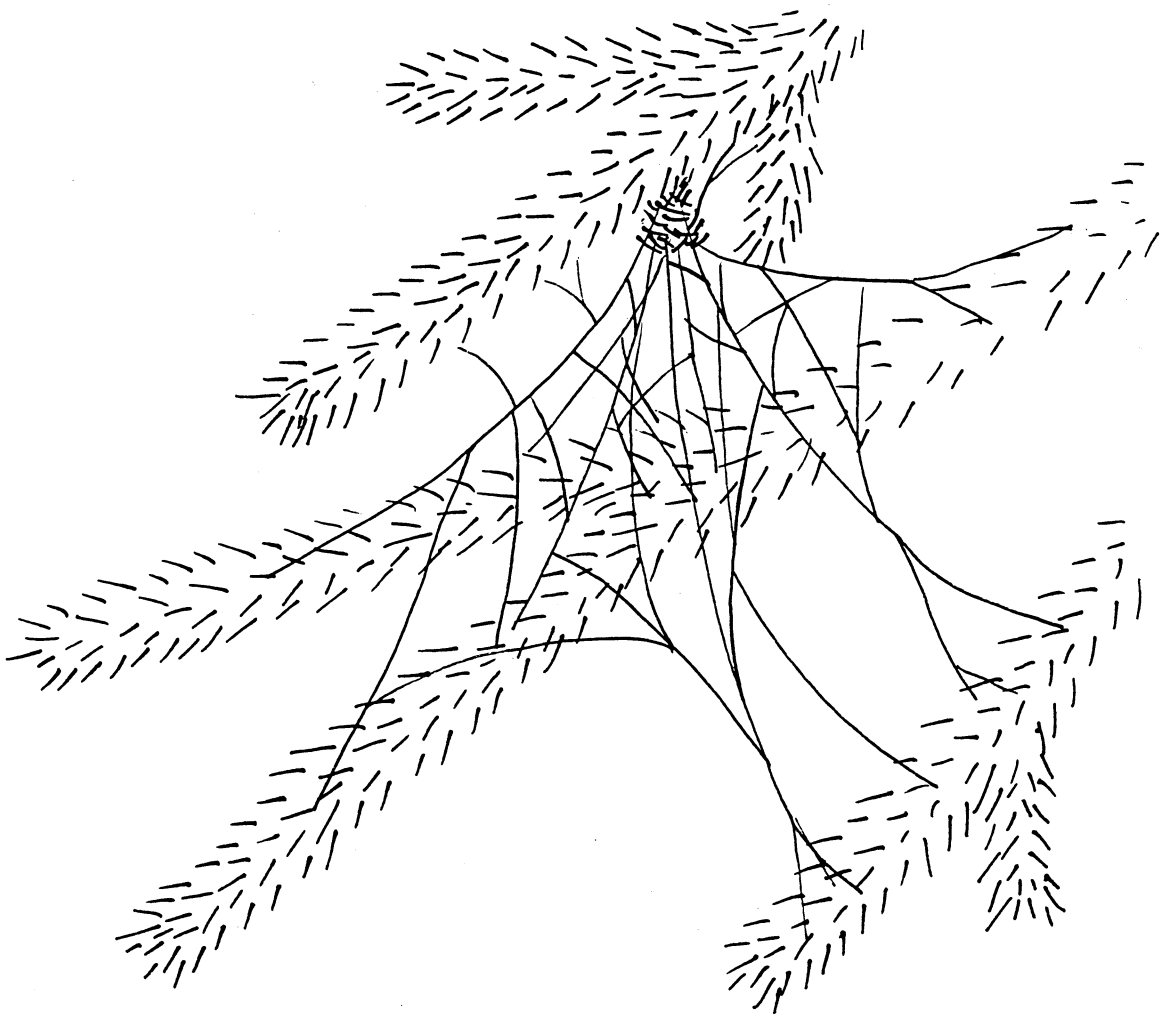


Figure 1.1 A drawing of a typical three-dimensional tangle web of *Theridion pictum*. Note the retreat at the apex of the web.

	1986			1987			
	Mean	N	Range	Mean	N	Range	P
Date of Egglaying	6/27	38	6/18 - 7/19	6/19	40	6/15 - 6/28	<.001
Date of Hatching	7/11	56	7/1 - 7/16	6/29	110	6/19 - 7/18	<.31
Duration of Incubation	14	30	10 - 17	15.3	23	10 - 23	<.001

Table 1.1. A comparison of the mean dates of egglaying, hatching and the duration of incubation of natural undisturbed webs in 1986 and 1987.

1986

Near	July 9 (18)
Medium	July 12 (16)
Far	July 20 (6)

July 12 (40)

1987

	Sunny	Dark	
Near	June 29 (10)	July 2 (32)	July 1 (42)
Medium	June 25 (18)	June 27 (14)	June 26 (32)
Far	June 30 (15)	July 1 (19)	July 1 (34)
	June 28 (43)	June 30 (65)	

Table 1.2. Mean dates of hatching of the first egg sacs, in each plot in 1986 and 1987. Near, medium and far refer to distances from the lake, a rich source of food in the spring and early summer. Sunny and dark are relative estimates of light intensity.

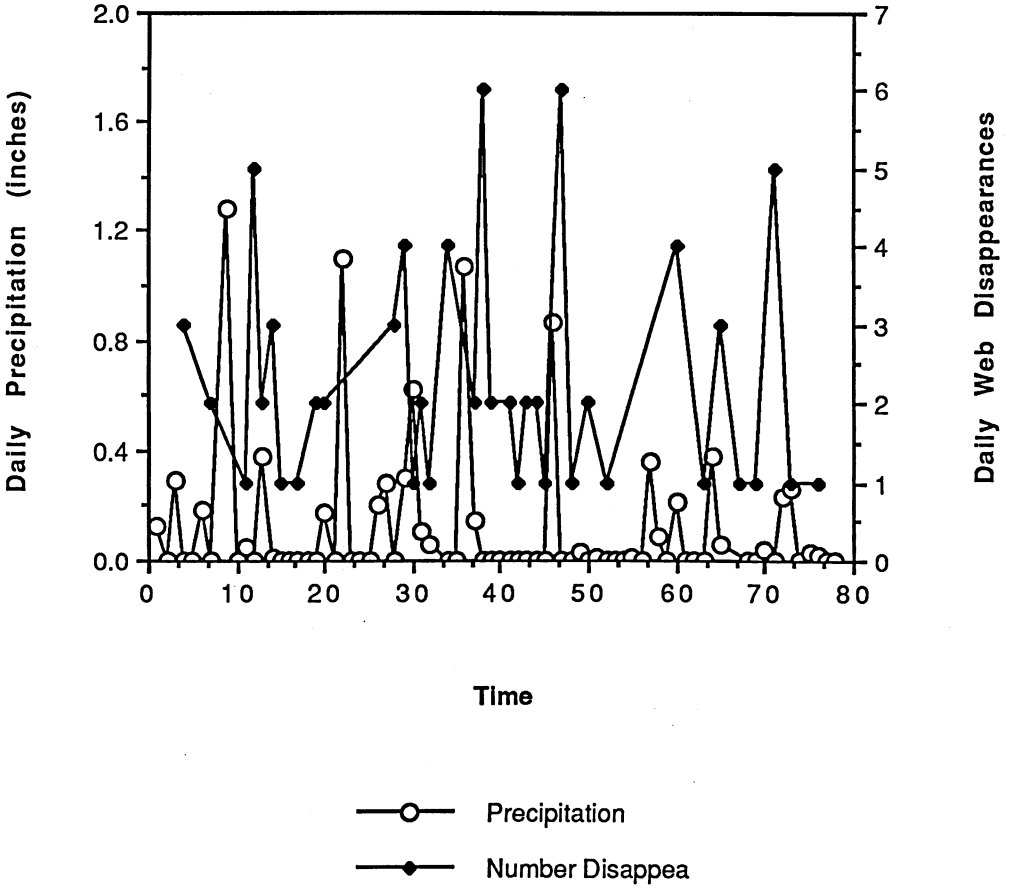


Figure 1.2. Web disappearances in relation to precipitation in 1986. The open symbols represent the daily precipitation in inches (left axis). The closed symbols represent the number of females that disappeared from their webs that day (right axis). The horizontal axis is the number of days since June 1, 1986. Note that large numbers of females frequently disappear the day after as well as the day of a heavy rainfall. This is an artifact of the rainfall occuring in the evening and my census picking up the disappearances the next day.

	1986		1987	
	n	%	n	%
Total Number of Marked Webs	108	100	175	100
Evicted by Another Spider	9	8.3	12	6.9
Parasitized by Wasps	3	2.8	9	5.1
Disappeared on the day of or the day after a rainfall	65	60.2	70	40

Table 1.3. Numbers and associated causes of deaths and disappearances of adult females in 1986 and 1987. The number of females parasitised by an Ichneumonid wasp is probably an underestimate in both years. In 1986 I did not initially recognize parasites and in 1987, observations were discontinued after July 30, one month earlier than in 1986. Disappearances correlated with rainfall are measured from June 16 through August 29 in 1986, and June 14 through July 18 in 1987. Thus, the 1987 figure is also an underestimate.

	1986 Wild Webs n = 29	1987 High Food n = 9	1987 Low Food n = 10
Days until fewer than 10 spiderlings remain	18.4	51.0+	37.9
Days until fewer than 2 spiderlings remain	32.2	56.4+	58.8
Number of spiderlings remaining on August 1	10.0	34.1	14.7

Table 1.4. Comparisons of the persistence time of undisturbed webs in 1986, and experimental caged webs in 1987 that were given either an abundant food supply (High food) or a limited food supply (Low food). Spiderlings do not disperse *en masse* hence there is no single time of dispersal. At the termination of the experiments in 1987, a mean of 20.6 spiderlings still remained in the 'High food' webs. Thus, 'days until fewer than 10 spiderlings remain' and 'until fewer than 2' are underestimates for this category. Furthermore, cages from the 1987 experiment that were affected by mold have not been removed. The majority of spiderlings in these cages died prior to the dispersal of spiderlings from other cages.

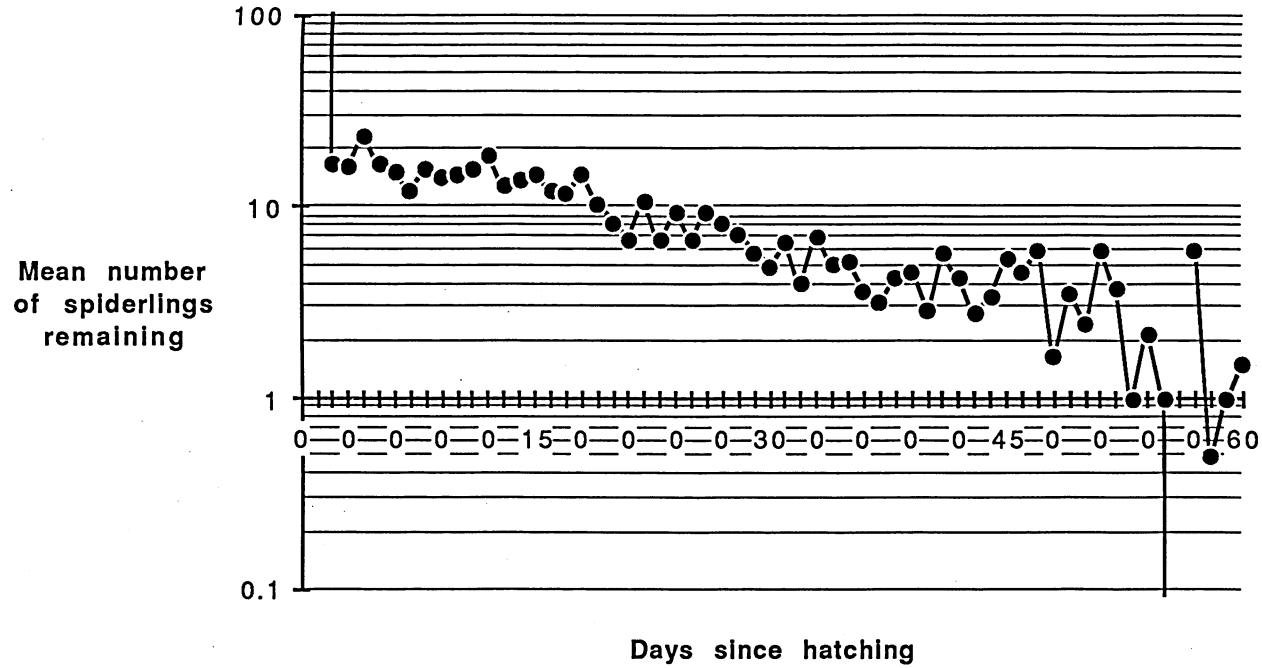


Figure 1.3. The mean number of spiderlings remaining in the web versus time since hatching, plotted on a semilog scale. Mean numbers of spiderlings were obtained from daily counts of individuals in undisturbed webs, (n is a mean of 11.4 webs with a range from 1 to 27). Note that webs that no longer had spiderlings are dropped from the sample. This is because spiderlings in these webs were forced to disperse when a spider of another species took over the web. Thus, data from empty webs do not represent a reduction in numbers due to voluntary dispersal or to siblicidal cannibalism. The increasing fluctuations in mean number over time is thus partly due to a decrease in sample size.

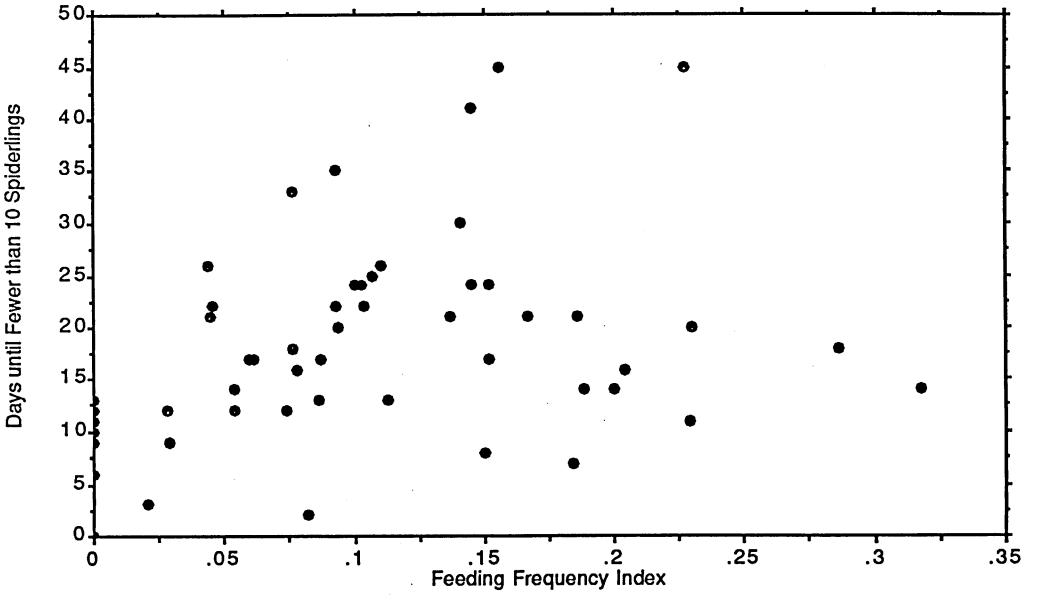
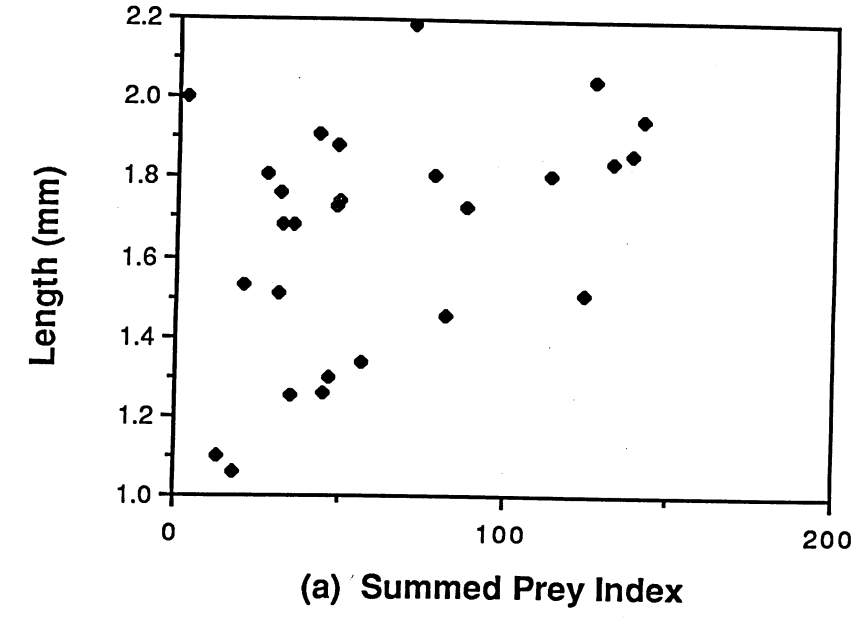


Figure 1.4. The relation between the 'feeding frequency index' and the number of days from hatching until fewer than ten spiderlings remain in undisturbed webs. Each point represents one web. Three points which had very high 'feeding frequency indexes' are not represented graphically but are included in the statistical treatment included in the text.



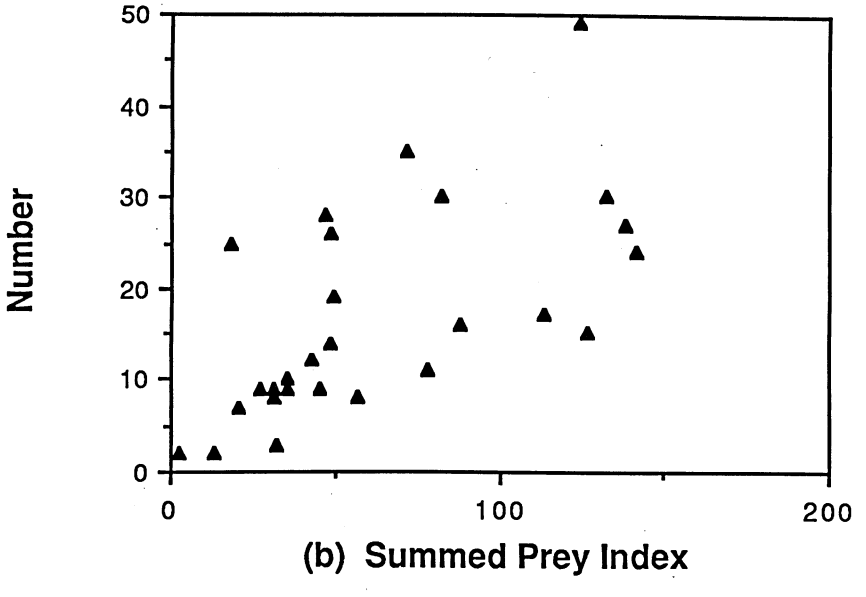


Figure 1.5 a,b. The 'summed prey index' versus (a) the length of spiderlings in mm. and (b) the number of spiderlings present, in the maternal web. Each point represents one web. The 'summed prey index' is the sum of the length of prey items (mm) that were found in the retreat of collected webs.

Chapter Two

EXPERIMENTAL MANIPULATIONS OF THE DISPERSAL BEHAVIOR OF THE SUBSOCIAL SPIDER, *Theridion pictum* (Walckenaer).

INTRODUCTION

Two scenarios are used to describe the evolution of social hymenoptera, and are also commonly used to describe the evolution of social arachnids (Shear 1970, Wilson 1971, Kullman 1972, Buskirk 1981). These are the parasocial route (Michener 1958), and the subsocial route (Evans 1958). The parasocial route begins with the aggregation of adults for any reason besides mating, and continues with the development of obligate cooperation leading eventually to an overlap of generations. In contrast, the subsocial route begins with an extension of the duration of maternal-offspring interactions, i.e. an overlap of generations, and eventually leads to cooperation between adults.

Theridion pictum (Walckenaer), is a subsocial spider belonging to the same family, Theridiidae, as several cooperatively social species. For this reason, it is a suitable species to study the subsocial route of evolution and in particular the role of environmental features as permissive or restrictive factors in social evolution. As there is already a large body of literature dealing with the effects of food distribution on social systems in arachnids (Turnbull 1964, Smith 1983, Rypstra 1985, Rypstra 1986, Krafft et al. 1986), and in other taxa (Emlen and Oring 1977, chapters in: Krebs and Davies 1984, Rubenstein and Wrangham 1986), and since the first step along a subsocial route is when some or all the offspring do *not* disperse, I chose to examine the role of food availability on the dispersal behavior of *Theridion pictum.*

In this paper, I present the results of experiments with caged female *T. pictum* and their offspring which were given either abundant or reduced amounts of food. Three aspects of the spiderlings dispersal behavior are examined. First, the temporal pattern

of dispersal. I predicted that spiderlings in cages given more food would remain longer on average. Since spiderlings are not dispersing to breed the same season, it is probably advantageous to remain at a site where food is already available rather than dispersing to an unknown site. Furthermore, dispersal may be less risky with increasing size or age.

Second, I present the quantitative patterns of dispersal. If spiderlings remain longer at food rich webs, then at any time there should also be absolutely more spiderlings remaining in the cages and hence, fewer dispersing. I also examine the pattern of disappearance, which is most likely the result of cannibalism (see below). When sufficient food is available disappearance (cannibalism) rates should be lower in food rich webs (Krafft 1986, Rypstra 1986).

The third aspect of spiderling dispersal that I examine is the occurence of any sex-bias in dispersal or philopatry. For theoretical reasons (Greenwood 1980), I predicted that females should generally be more philopatric than males, and that, dispersal would be male-biased. Animals with resource defense mating systems, such as most birds, usually show female-biased dispersal. Greenwood (1980) argued that inheritance of a familiar territory in such species can improve a male's mating success relatively more than a female's. In contrast, most mammals have polygynous mating systems with males wandering in search of mates and with females providing the majority of the parental care. In this situation, male-biased dispersal is the general rule. Males should be able to obtain more matings by defending females rather than a territory. In addition, females may be able to provide superior parental care if they are in a familiar territory or range. Thus, I had predicted that spiders, including *T.*

pictum, would show a pattern similar to mammals. Like mammals, most male spiders typically wander in search of females and may guard them, rather than food resources, from other males (e.g. Austad 1983). Furthermore, in many spider species, the adult male never builds a web or captures prey and the female provides all, if any, parental care.

METHODS

These experiments were conducted during the summer of 1987 on the grounds immediately adjacent to The University of Minnesota Forestry and Biological Station in the Lake Itasca State Park, Minnesota. For the purpose of artificially manipulating food availability and to separate dispersal from cannibalism, twenty cages were built, each measuring 18"x18"x12". Three sides were faced with plexiglass to facilitate viewing the spiders and three sides were faced with wire screening to allow air currents to pass through, (see figure 2.1). This wire screening was also coated with Tanglefoot™, a commercial tree-banding adhesive, to prevent very small spiderlings from escaping. Each of these cages was divided into an inner and an outer compartment by screening with holes punched in it, allowing spiders of all sizes to leave the inner compartment and enter the outer compartment. A web support structure constructed of thin dowels was placed inside the inner compartment of each cage. The cages were arranged in two staggered rows of ten on a scaffold located in a wooded area near the station and an opaque black plastic roof was suspended 4-5 feet above the cages to exclude rain and to provide shade.

On May 23, a single mature female *T. pictum* was dropped onto the web supports

of each cage. Females were only allowed to build their webs inside the inner cage. Any females that tried to weave webs in the outer cage had their webs destroyed and were placed back into the inner cage. This process had to be repeated several times for some females. One to two weeks later, a single male was added to each cage to ensure that each female had the opportunity to mate. All of these males were either eaten or found dead in the web shortly thereafter.

Five cages on the upper level and five on the lower level of the scaffold were randomly chosen and assigned the 'high food' treatment. The remaining ten cages were assigned the 'low food' treatment. Prior to the beginning of treatment, spiders were fed ad lib with mayflies, caddisflies, mosquitos and small moths (Orders; Ephemeroptera, Trichoptera, Diptera and Lepidoptera), which were caught in a light trap near the lake. At any one feeding I tried to select twenty of the same item, (such as twenty small, pink, moths). When this was not possible I chose twenty similarly weighted sets of items (for example, two small Diptera might equal one Trichoptera). At all times throughout the season, prey items were weighed and then randomly assigned to cages. When possible, I also preferred to give cages fewer, larger items rather than many, small items. This was for two reasons. One, I could tell whether the spider had caught what I had provided. When many small items were provided I could not be sure exactly how many prey items the spider had caught. Thus, if a spider did not catch it's morning prey item, I frequently gave it a second item in the afternoon. Two, it was easier to count spiderlings feeding on a large item. As the season progressed, frequent rainfall prevented me from collecting food with a light trap hence I switched to netting damselflies (Odonata). The use of damselflies was preferable over mixed insects for one

additional reason: providing a single very large, but long prey item prevented one or a few spiderlings from monopolizing the food.

Treatment of each cage began one week after the hatching of the first egg sac in that cage. Since egglaying and hatching did not occur on the same day in all cages, the beginning of treatment differed between cages; the start of treatment of all but one cage began within 12 days of each other. Low treatment webs were initially given an amount of food believed necessary to sustain one adult spider; the wet weight of the prey was approximately equivalent to an adult female spiders weight. This estimate was based on observations of feeding behavior during the summer of 1986. In retrospect, I think this estimate was high and thus low treatment webs received an amount of food comparable to what wild spiders capture in a good site. However, this amount gradually decreased just as the amount given to high treatment cages increased, (Figure 2.2). Initially, high treatment cages were simply given a second feeding each day. With the switch of food from mixed insects to damselflies this changed. At first, I decreased the level of provisioning to the low treatment cages by giving all webs the mixed food every other day and giving damselflies only to high treatment webs on the off days. Shortly thereafter, I began to provide only damselflies to all webs but gradually increased the number of days between each feeding of low treatment webs. By August this feeding schedule had stabilized at one damselfly per week for low treatment webs and seven damselflies (with the occasional dragonfly) per week for the high treatment webs. By the end of the season the 'high food' webs were receiving about ten times the amount of food, in wet weight, as the 'low food' webs.

The cages were monitored nearly every day from June 14 until August 28. This

included recording whether any new egg cases were laid or hatched, and as soon as possible after hatching, counting the numbers of spiderlings present. I also carefully examined the outer cage for any dispersing spiderlings. Spiderlings found in the outer cage were removed, scored as having dispersed on that date, and preserved in 75% isopropyl alcohol. Later, I measured the tibia plus patella of one of the first pair of legs of each individual. I found that I was able to determine the sex of spiderlings whose first tibia plus patella was longer than .75 mm . At this stage, the males already have very clearly swollen pedipalps.

During the course of treatment, a few cages became contaminated by mold or fungus. Within just a few days of the first noticeable growth on carcasses, nearly all the spiderlings in each of these cages were covered by growth and were dead. Because this event terminated the experiment in these cages well in advance of other cages, and because I could not know whether the fungus/mold affected the spiderlings' behavior prior to its visible appearance, I have excluded these cages, (1, 3, 8, 14, and 15), from analysis. I have also excluded web 5 from analysis. This is because just 5 days after the spiderlings hatched, the mother abandoned the web. The web she left behind was not extensive enough for the spiderlings to catch their own food.

On September 12, the cages were cleaned out and all remaining spiderlings were collected, counted, measured and sexed. In addition, the empty egg cases in the retreats of all but two cages were removed. From each egg case, I removed and counted the number of egg shells, unhatched eggs, exuviae from the spiderlings' first molt, and dead spiderlings. I was also able to calculate the total number of spiderlings which disappeared from each cage over the whole season by subtracting the total number of

spiderlings accounted for (the number collected from the cages on September 12, plus the total number of dispersers) from the combined number of exuviae found inside the two egg sacs of each cage; this latter figure is a good estimate of the number of spiderlings emerging from the egg sac.

Insects were identified using Borror and White (1970). Identifications of *T. pictum* voucher specimens were made by Dr. Herbert Levi and placed in the collection of the Harvard Museum of Comparative Zoology. Additional identifications of spiders were possible using Levi (1957) and Kaston (1953).

RESULTS

Temporal patterns of dispersal

In theory, the mean persistence time for each cage is simply the mean number of days that each spiderling spent in the maternal web, the average taken over all spiderlings dispersing from that cage. In practice, these calculations had to be modified because I could not tell whether a given spiderling hatched from the first or the second egg sac. Thus, I used the mean date of hatching as the hatching date for all spiderlings of a given cage. I found that the mean persistence time of cages given the low food treatment were significantly shorter than those given the high food treatment (Mann-Whitney $U=2$, $N_1= 6$ $N_2=8$, $P<.01$), (figure 2.3). This is especially notable when one considers that not one single spiderling dispersed from cage 7, (a high food treatment cage), and hence a mean persistence time of 60 days for this cage is an underestimate.

Quantitative patterns of dispersal

Besides remaining longer, significantly fewer spiderlings dispersed from the high food treatment cages, (Mann-Whitney $U=2$, $N_1=5$ $N_2=8$, $P<.05$), (Table 2.1 and Figure 2.4). In turn, significantly more spiderlings remained in the high treatment webs at the end of the experiment, (Mann-Whitney $U=0$, $N_1=5$ $N_2=8$, $P<.01$). These findings are equally true of both sexes. Females are significantly more likely to disperse from than to remain in low treatment webs, and to remain in rather than to disperse from high treatment webs, (Chi-square = 193.2, d.f =1, $P<.001$). The same is true of males, (Chi-square = 47.3, d.f.=1, $P<.001$), (Table 2.2).

I also compared the total number of disappearances between treatments. Significantly more spiderlings disappeared from low food treatment webs, (Mann-Whitney $U=5$, $N_1=5$ $N_2=7$, $P<.01$), (Table 2.1 and Figure 2.4). While this group must technically be referred to as disappearing since I did not observe what happened to them, I believe most were cannibalized. I have observed at least one occurence of cannibalism in natural, undisturbed webs and one in the cages. Furthermore, if these spiderlings had died for other reasons their uneaten bodies would have been visible in the web, whereas carcasses that had been sucked dry would have been very difficult to see and most likely would have been overlooked.

Disappearance, or cannibalism, is probably also occurring even before spiderlings reach their first molt inside the egg sac. Significantly fewer spiderlings from the second egg sac reach their first molt than do spiderlings from the first egg sac, (Mann-Whitney $U=0$, $N_1=12$ $N_2=12$, $P<.01$), (Table 2.3). I suspect this difference

was due primarily to cannibalism of second sac spiderlings by first sac spiderlings. I also looked for any difference between treatments in the number of second sac spiderlings that disappeared before hatching; treatment could not have affected the number that disappeared from the first egg sac, but it may have affected the number that disappeared from the second egg sac. This is a consequence of beginning treatment one week *after* the first sac spiderlings emerged and approximately one week *before* the second sac spiderlings emerged. I had thought that spiderlings receiving less food might cannibalize more of the eggs, however, there is no significant difference in the disappearance rate of pre-emergent second sac spiderlings between treatments, (Mann-Whitney $U=11.5$, $N_1=5$ $N_2=7$, $P<.25$). It may be that the very young first sac spiderlings were not yet food limited or that the effects of treatment were not felt at the end of one week.

I have also looked for correlations between the probability of dispersal and of disappearance, under each treatment. The probability of dispersal is calculated as the sum of the number of spiderlings that dispersed from either the high or the low treatment, divided by the sum of the number of spiderlings that were present on the previous day in the respective cages. The probability of disappearance is calculated similarly. In addition, I taken averages for each treatment using both a real time scale (T1) and using an adjusted time scale where all cages hatch the same day (T2). There was no significant correlation between dispersal and disappearance from cages provided the high treatment or the low treatment, using either time scale (Table 2.4).

Sex-biased dispersal and philopatry

In Table 2.5, I have summarized the data on the numbers of dispersing and

remaining spiderlings of each sex, under each treatment. It should be noticed immediately that the sum of the number of females dispersing plus the number remaining is twice the sum of males dispersing and remaining. Three explanations can be proposed to explain this female biased sex-ratio. One, there is a female-biased sex-ratio at birth, two, there is male-biased cannibalism and three, I have incorrectly sexed spiderlings. Circumstantial evidence allows me to rule out the last case with some confidence. The most probable reason for incorrectly sexing spiderlings would be that I have included some as yet undeveloped males in with the females. However, if I had mistakenly included some of the small males in with the females, I would expect the sex-ratio of the low treatment spiders to be more female biased than the high treatment spiders. Low treatment spiderlings are, overall, significantly smaller than the high treatment spiderlings, (Mann-Whitney $U=5478.5$, $N_1=198$ $N_2=246$, $P<.0001$). While only 108 of 169 (63.9%) of the low treatment spiderlings are females, 142 of 200 (71.0%) of the high treatment spiderlings are females. Thus, there is actually a higher percentage of females in the high food treatment group. I take this to imply that I have not made any large scale errors in sexing spiderlings.

The remaining explanations are that there is either a bias in sex-ratio at birth, or male-biased mortality. Female-biased sex ratios are known to occur in one cooperatively social species belonging to the same family as *T. pictum*, this is *Anelosimus eximius* (Vollrath 1986). It is interesting that this bias decreases with the growth of *A. eximius* spiderlings, apparently because of female, rather than male, biased mortality. This would suggest then, that there is a female biased sex ratio at birth rather than male-biased mortality, however, at this time I cannot conclude that

the sex-bias is the result of either cause.

If a female-biased sex ratio at birth does occur in *T. pictum* , one explanation may be that parental investment in males is greater than in females (Trivers and Willard 1973). Although females are the larger sex at maturity, males remaining in the cages at the end of two months are larger than females (Mann-Whitney U=910, N_1=17 N_2=180, P<.01). The end of two months might be a reasonable estimate of the end of parental investment since only 5 of 20 mothers were still alive at this time. However, an exact correspondance between size, i.e. investment, and sex-ratio is not observed; males are not twice as large as females while females are twice as common as males.

Although males collected from the cages at the end of the experiment were larger than females, the relative difference in sizes varied between treatments. Males from the low treatment are 9.6% larger than the corresponding females (Mann-Whitney U = 17, N_1=5 N_2= 12, P<.15), whereas high treatment males were 26.1% larger than females (Mann-Whitney U=1014.5, N_1=48 N_2=132, P<.0001) (Table 2.6).

Regardless of the reason for the sex-bias, I wish to ask whether there is any difference in the relative proportions of males and females which remained or dispersed under each separate treatment. I find that although both sexes are more likely to disperse than to stay under the low treatment, females are relatively more likely to disperse than males (95.4% vs. 80.3%), (Chi-square= 9.75, d.f.=1, P<.005), (Table 2.5). In contrast, under the high treatment, both sexes are more likely to stay than to disperse, however females are relatively more likely to stay than males (93.0% vs. 82.8%), (Chi-square = 4.76, d.f.=1 P<.05).

I have also compared the rates of survival of females and males, prior to dispersal, by comparing the combined number of dispersing and remaining individuals of each sex, under each treatment. Under the high treatment, there are relatively more surviving females than males while under the low treatment there are relatively fewer surviving females, although this result is not statistically significant (Chi-square=2.11, d.f.=1, $P<.25$). Thus the survival rate of females, prior to dispersal, may be more sensitive to food availability than that of a males but this is not convincingly demonstrated by these data.

DISCUSSION

Evolution of sociality

Experimental results indicate that *Theridion pictum* spiderlings remain at the maternal web longer and in greater numbers when more food is available. Evidence from natural webs (see chapter one) also indicates that spiderlings remain longer when more food is available. These results provide support for the importance of food availability as a permissive factor in social evolution, and also for the subsocial route to sociality. If for some reason, there is a net advantage to remaining in the maternal web, spiderlings may persist at the web for longer and longer periods. In an environment with abundant food resources and without the constraining feature of cold winters, spiderlings might eventually forego dispersal altogether. This is the first step toward sociality.

Some advantages of remaining at the maternal web include avoiding the presumably dangerous process of dispersal; most web spinning spiders have little facility for

detecting anything once they are out of their webs. Advantages could also include sharing the costs of web spinning, retreat construction, and prey capture. Nentwig (1985) argues that one advantage of sociality in spiders is to capture larger prey. However, Packer and Ruttan (1988) argue that for most species, the ability of a group to capture larger prey is likely to be a resultant advantage of sociality rather than a causal factor. One exception however, might be in groups of highly related individuals, as in many species of cooperatively social spiders. However, there are also costs associated with grouping. For example, Smith (1982) has found that colonies of *Philoponella oweni* living in areas of high food abundance, are also subject to higher rates of egg case parasitism by wasps than are solitary individuals living in poorer areas.

While there may be a direct benefit to spiderlings from having more food available, the indirect effect of reduced rates of cannibalism may also be critical in determining whether they disperse or not. After the start of this research program, two papers were published which argue a similar point. Both papers stress food availability as a mechanism to increase tolerance levels (Krafft 1986), or conversely, to suppress cannibalism (Rypstra 1986). I have attempted to separate out the effects of food deprivation and cannibalism by looking for correlations between the rates of cannibalism and the rates of dispersal. I had expected that increased rates of dispersal would be associated with increased rates of cannibalism. Unfortunately, I was not able to discern any pattern of dispersal in relation to cannibalism whatsoever due to the inaccuracy of my daily spiderling counts.

Sex-biased dispersal

Although I have found that females are relatively more philopatric than males when

food is plentiful, my results also indicate that dispersal is relatively female biased when food is not plentiful. These patterns of dispersal and philopatry seem to indicate that females are generally more sensitive to food availability than are males. Likewise, there is a trend for female survival prior to dispersal to be more sensitive to food availability than is male survival. These results are consistent with the observation that mature females are larger than males and hence, female reproductive success is expected to be more dependent on food availability than that a male's. Research on other taxa supports this expectation. Howard (1988) has compared the lifetime reproductive success of two anurans with differing degrees of sexual dimorphism; the woodfrog (*Rana sylvatica*) a species with larger females, and the bullfrog (*Rana catesbeiana*) where both sexes are about the same size. His findings indicate that the lifetime reproductive success of bullfrogs is independent of size, while for woodfrogs, female lifetime reproductive success does increase more rapidly with size than does a male's and thus is highly size dependent.

However, I have also found that male *T. pictum* may be more sensitive to food availability in one respect at least. That is, male growth rates during the first two months appear to be more dependent on food availability than are female's growth rates. When more food is available males grow faster than females relative to low treatment spiderlings. Two reasons may explain this surprising result. First, this may be an artifact of only comparing the final size of spiderlings that have not dispersed or died. If small females disperse prior to large females, as I have suggested in chapter one, a greater proportion will have dispersed from the low treatment webs. This would inflate my measurement of the mean size of low treatment females and in turn, it would then

appear as if low treatment males were not growing as rapidly as high treatment males. However, then one must ask why the size of females is not equally inflated. Second, one must consider the long term growth rates and mating strategies of each sex. Regardless of whether males are larger in the fall, at maturity females are larger than males. However, there may not be the same pressure for females to grow as rapidly. While it is difficult for females to assess the quality of a web-site prior to reproduction, it may be relatively easy for males. They must look for an area with many females. A male that develops quickly may have enough time to disperse multiple times in his search for females or alternatively may be large enough to defend access to his sisters.

It would be very interesting to obtain data on sex-biased dispersal in other populations and other species of spiders to test whether these dispersal patterns are common to other species of spiders. Furthermore, we need to confirm that the lifetime reproductive success of female spiders increases more rapidly with size than does a male's. To my knowledge, the only other information on the sex of dispersing spiders comes from work on cooperatively social species. While dispersal seems to be a generally rare event, it is usually by gravid females (Aviles 1986, Vollrath 1982, Lubin and Robinson 1982, Christenson 1984), or not at all. Roeloffs and Riechert, (1987), have not found any evidence for the active dispersal of either sex of *Agelena consociata* . There is movement between connected but separate segments of nests however. One could hypothesize that there may be patterns of dispersal within the colony, however there has been no substantial work on this topic or in fact, on dispersal generally.

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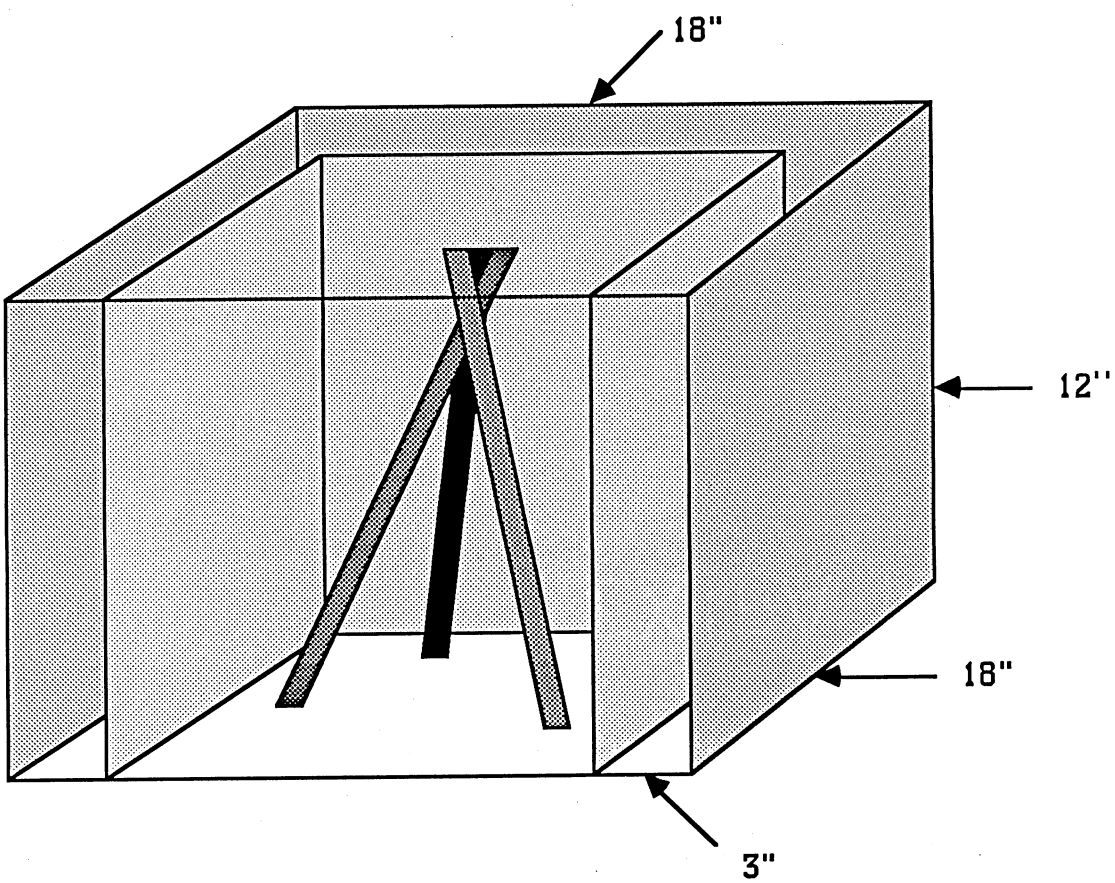

Figure 2.1. A schematic drawing of an experimental cage. The top, bottom and front were faced with plexiglass to facilitate viewing and the three remaining sides were faced with wire screening to allow ventilation. The top pane of plexiglass could be lifted to introduce food to the cage. An inner cage was separated from the outer cage by wire screening with holes punched in it. This allowed spiderlings free passage to the outer cage. However, the outer cage was coated with a sticky substance to prevent spiderlings from escaping. A web support structure constructed from thin wooden dowels was placed in the inner cage.

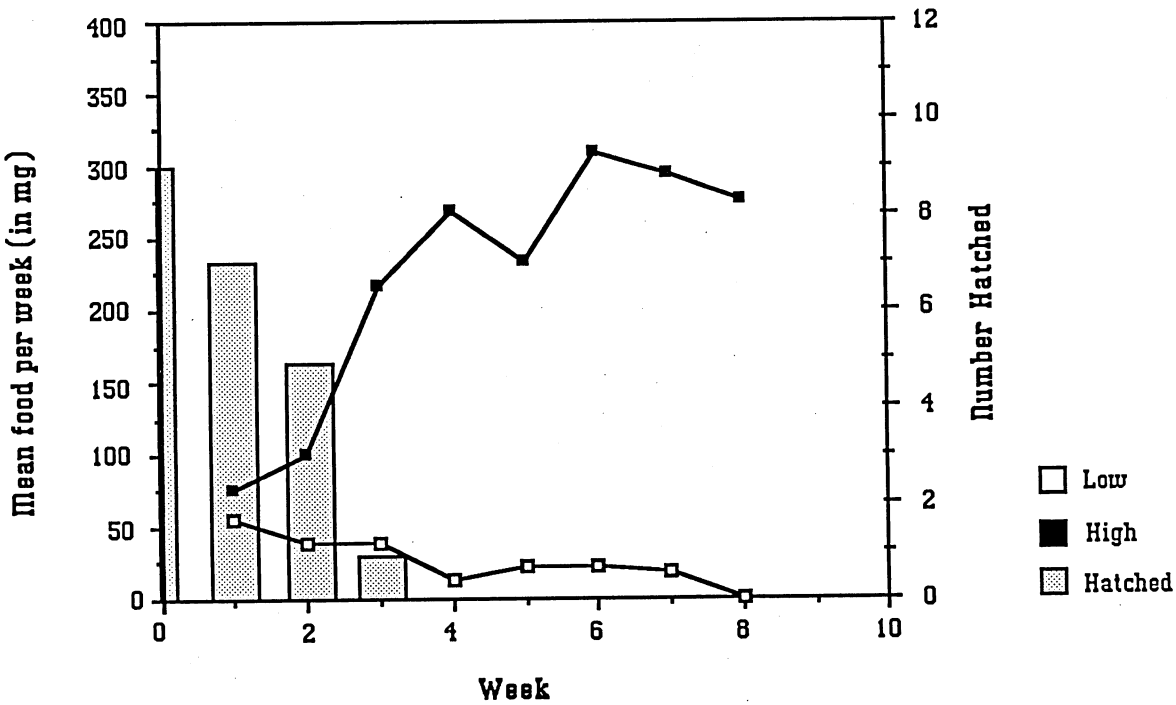

Figure 2.2. Comparison of the amount of food provided per week to cages given the high food treatment versus cages given the low food treatment. Each point represents the mean of the sum of food provided over one week, in mg., to either high food or low food cages. The columns represent the number, each week, of cages with newly hatched spiderlings.

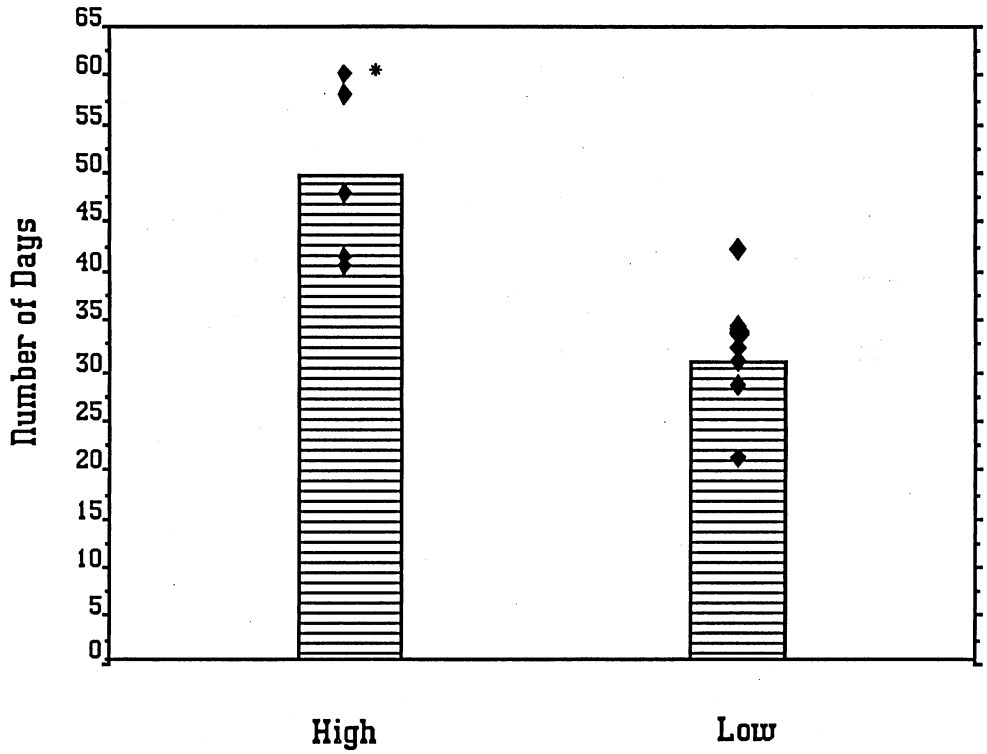

Figure 2.3. The mean persistence times of cages given either an abundant food supply (High food) or a limited food supply (Low food). Each point represents the mean persistence time of one cage, which is the mean of the number of days between hatching and dispersal, the average taken over all spiderlings which dispersed from that cage. The columns represent the mean for each treatment. One cage, marked with a *, was provided the 'High food' treatment and did not have a single dispering spiderling. Thus, 60 days is a lower bound. Cages that were infected by mold were excluded.

	High			Low			
	Mean	Range	n	Mean	Range	n	P
Exuviae	54	33-81	5	60.29	24-85	7	n.s.
Dispersed	4.6	0 -12	5	22	9 - 45	8	<.05
Remaining	36.4	18-49	5	2.13	0 -7	8	<.01
Disappearances	13.2	0 -21	5	41.86	13-71	7	<.06

Table 2.1. Comparison of the mean number, in each treatment, of spiderlings that dispersed, spiderlings remaining in the cages on September 12, disappearances since emergence, and exuviae found in the egg sacs. Exuviae are from the spiderlings' first molt, which occurs inside egg sacs. This number estimates the actual number of spiderlings emerging from an egg sac. Cages that were affected by mold were excluded.

	Disperse	Remain	Chi-Square	P
Female:				
Low	103	5		
			193.2	<.001
High	10	132		
Male:				
Low	48	12		
			47.3	<.001
High	10	48		

Table 2.2. Numbers of spiderlings from each treatment that dispersed or remained, in the cages as of September 12, separated by sex. 'High' refers to cages that were given an abundant food supply and 'Low' refers to cages that were given a limited amount of food. Cages that were affected by mold were excluded.

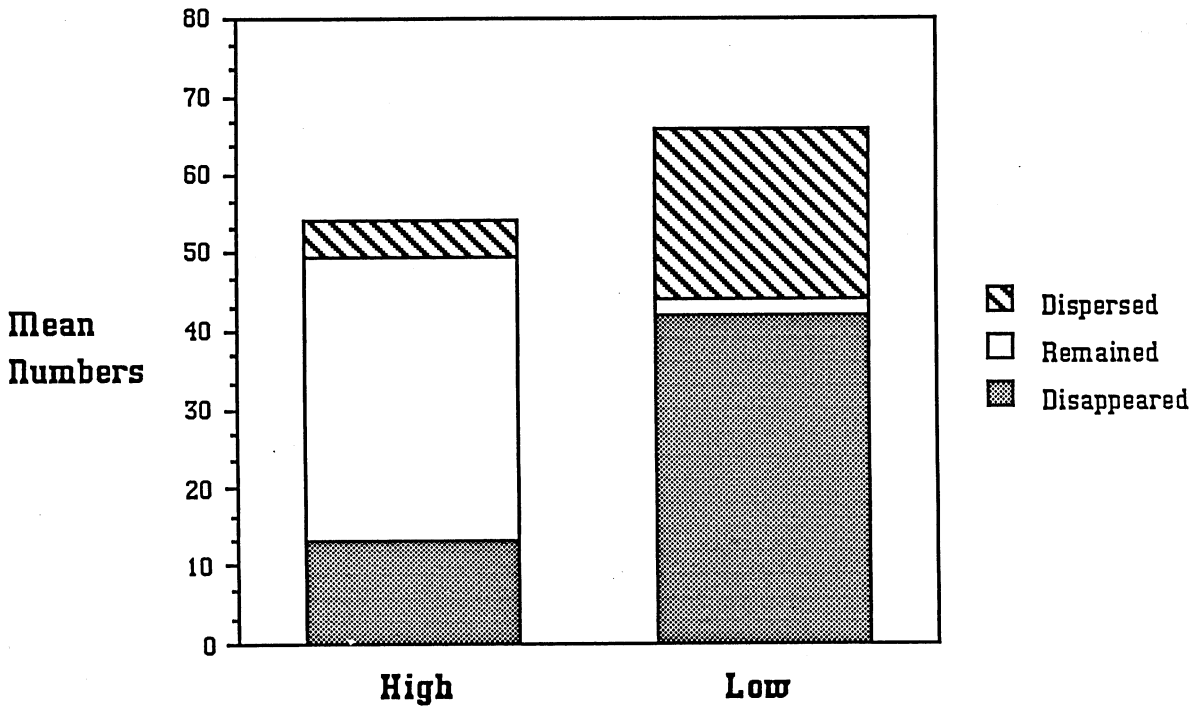

Figure 2.4. Graphical comparison of the numbers spiderlings which dispersed, remained and disappeared from cages given either an abundant or a limited food supply. Statistical comparisons are presented in Table 2.1.

	High		Low		Kruskall-Wallis	P
Eggshells:						
First Egg Sac (n)	69.0	(8)	66.4	(9)		
					3.038	n.s.
Second Egg Sac (n)	67.3	(8)	81.7	(9)		
Exuviae:						
First Egg Sac (n)	50.5	(8)	56.2	(9)		
					24.195	<.005
Second Egg Sac (n)	5.0	(8)	6.1	(9)		

Table 2.3. Comparison of the mean number in each treatment, of eggs laid in the first and second egg sac, of eggshells in the first and second egg sac, and of exuviae from the first and secong egg sac. Cages that were affected by mold were not excluded.

	High			Low		
	Rho	n	P	Rho	n	P
T1	-0.062	60	<.36	0.044	60	<.38
T2	-0.008	60	<.40	0.073	60	<.34

Table 2.4. Spearman's rank correlations between the probability of dispersal and the probability of disappearance using two time scales; a real time scale (T1), and an adjusted time scale where all cages hatch their first egg sacs the same day (T2).

	Disperse	Remain	Chi-Square	P
High:				
Female	10	132		
			4.76	<.05
Male	10	48		
Low:				
Female	103	5		
			9.75	<.005
Male	48	12		

Table 2.5. Numbers of spiderlings of each sex that had dispersed or remained in the cages as of September 12, separated by treatment. 'High' refers to cages that were given an abundant food supply and 'Low' refers to cages that were given a limited amount of food. Cages that were infected by mold have been excluded.

	High Treatment		Low Treatment	
	Female	Male	Female	Male
Mean	1.25	1.57	1.12	1.23
n	132	48	5	12
S.D.	0.19	0.27	0.05	0.19

Table 2.6. Length of the first tibia plus patella (in mm.) of male and female spiderlings remaining in the cages as of September 12. Cages were given either an abundant amount of food (High food) or a limited amount of food (Low food). Cages that were infected by mold have been excluded.

Chapter Three

DISCUSSION

In this chapter, I discuss my results in the context of the evolution of sociality. First, I examine how sociality has evolved in spiders and discuss the relative importance of subsocial versus parasocial routes of evolution. I then argue that my results support the scenario of subsocial evolution for the Theridiidae. Finally, I speculate on the reasons that subsociality may have evolved in *Theridion pictum* .

Types of Sociality

Sociality has been defined in many different ways, frequently depending on the taxa that the researcher usually studies. If all researchers were to use the criteria of entomologists, that of eusociality, then outside of the insects the only other animal to qualify would be the naked mole rat. For other taxa however, less stringent definitions may have more usefulness. Certainly a lion is social when compared with a cheetah, or a scrubjay compared with a crow. I restrict my use of the term social to any species whose adult members spend a portion of their life together, other than for the sole purpose of mating. Species where a single adult cares for its young for an extended period after hatching will be referred to as subsocial. In addition, I will distinguish two types of social system; gregarious, and cooperatively social, (Buskirk 1981). The former are sometimes referred to as colonial or semisocial, however, the use of the term gregarious facilitates comparisons between spiders and vertebrate taxa. In Table 3.1, I have summarized some available information on the behavior of species that will be mentioned in this chapter.

Gregarious species of spiders live in a restricted area, i.e. a colony, and frequently share structural web support lines and sometimes even a retreat. They typically do not

share capture webs. Different individuals may weave webs at the same site at different times, or there may even be piracy of a web (Burgess 1976, Lubin 1974) but individuals usually do not share the web or the food caught there. Typical examples of gregarious species are the facultatively gregarious *Philoponella oweni* (Smith 1982), and the obligately gregarious *Metabus gravidus*, (Buskirk 1975).

Cooperatively social species have a stable and obligate social structure as adults and cooperate in web building, hunting, and care of the young. They also have overlapping generations which live and breed in the same colony. Colonies are frequently very large with hundreds or even thousands living in a single web (Buskirk 1981). Species from four families occur in this category. These are the Agelenidae, the Dictynidae, the Eresidae and the Theridiidae. Two of the better studied species are *Agelena consociata* (Agelenidae) (Krafft 1970, Riechert 1986), and *Anelosimus eximius* (Theridiidae) (Brach 1975, Vollrath 1986).

One species that does not fit neatly in either the gregarious or the cooperative category is the orbweaving *Eriophora bistriata* (Araneidae). Several individuals that inhabit separate but adjoining webs may cooperate to capture 'very large prey' (Fowler and Diehl 1978). Furthermore, the whole colony shares a single daytime retreat as well as webbing support lines. If it were not for their habit of cooperating to capture very large prey they would easily fit in with the gregarious species. Yet they cannot be easily placed with the cooperative species since they do not cooperate in brood care, maintain a single web or have overlapping generations. Technically, they do not even qualify as social, since these colonies are composed of groups of juvenile siblings which disperse after maturing, and neither are they subsocial since the mother dies prior to

the spiderlings' hatching. However, Fowler and Diehl indirectly indicate that the juvenile phase is by far the longest part of the life cycle. I have chosen to include them with the gregarious species, primarily because of the lack of cooperation during the adult phase.

It is interesting to note that cooperative sociality has only evolved in families of spiders which weave three-dimensional sheet or tangle webs. There seem to be important constraints operating on orbweavers, preventing cooperative forms of sociality from evolving (Buskirk 1981). Peters (1970) has noted that orb webs can only be built by one individual. In contrast, three-dimensional webs can be added onto by any individual, at any time. Buskirk (1981) further notes that the design of an orb web means that only one individual at a time can hunt efficiently. Vibrations from the prey are passed down the radii to the hub, where they are monitored by the spider. Only one individual at a time can occupy the hub and still be able to localize the direction from which the vibrations arrive. As mentioned above, *Eriophora bistriata* is an exception to this. It may be that the 'very large prey', which they cooperate to capture, sets up large vibrations that resonate in adjoining webs and makes it easy for several individuals to locate the source. In contrast, the vibrations of an insect landing in a sheet or tangle web do not converge on a single point, or 'hub'. Thus, many individuals can simultaneously monitor the arrival of insects.

Gregariousness is much more common among orbweavers, and comparatively rarer among sheet and tangle web weavers. It may be that the three-dimensional structure of sheet and tangle webs make it difficult for colonial individuals to maintain the integrity of their own boundaries in a colony. There is frequently no distinction

between support and capture lines. Besides not being able to distinguish their own web, individuals may not be able to identify their own offspring. One marked female *T. pictum* that I observed, fell into another spider's web, evicted the original mother and continued to provide parental care for the other's spiderlings. Other authors have also commented on the apparently very limited capacity of spiders to recognize conspecific individuals (Kullman 1972, Burgess 1976).

Thus, where conditions lead to aggregations of spiders, orbweavers will develop gregarious forms of sociality whereas sheet and tangle web weavers will more commonly develop cooperative sociality.

Evolution of Sociality

As described in the last chapter, two routes of evolution have commonly been used to explain how sociality has evolved in insects; these are the subsocial route (Evans 1956), and the parasocial route (Michener 1956). Recall that evolution along a subsocial route occurs through an extension of the maternal offspring bond leading first to an overlap of generations and eventually also to multiple adults per colony. In contrast, evolution along a parasocial route begins with the aggregation of adults and eventually results in the overlap of generations. While some arachnologists argue that these models can be appropriately extended to spiders, others argue a hybrid of the two more appropriately descibes the unique spider system (Shear 1970, Buskirk 1981). I think part of the confusion results from a semantic problem. Do groups of siblings remaining in the same location after the mother has died constitute a parasocial or a subsocial grouping? Michener's writings do not provide an easy answer to this

problem. This is because of one basic difference between the lifecycle of wasps and of spiders. While wasps may *return* to the parental burrow and aggregate there while they lay eggs, spiders do not return once they have dispersed. However, for both wasps and spiders it appears that the most common aggregations of adults are actually sibling groups (wasps: Brockman 1984, spiders: Buskirk 1981, Lubin and Robinson 1982, Vollrath 1982). Thus, the real difference between the first step of a subsocial and parasocial route may simply be the presence or absence of the mother. Species where groups of sibling spiders remain together in the absence of the mother should be considered part of a parasocial pathway rather than a subsocial pathway.

It seems fairly clear that cooperative sociality has evolved along a subsocial route in three families; the Theridiidae, the Agelenidae and the Eresidae (Kullman 1972, Shear 1970). In all three of these families there is a clear gradient of sociality beginning with solitary species, through species where the mother takes care of the young, and leading to social species where adults cooperate in brood care as well as in hunting and web construction. The colonies of most of these species are also founded by only one or a few females and thus are highly endogamous, i.e. may be considered an extension of the subsocial system. My results support these conclusions and further, suggest a mechanism by which sociality may have evolved. In both an experimental setting and in a natural setting, spiderlings remain longer in the maternal web when more food is available. Furthermore, disappearances which are probably due to cannibalism (siblicide), are less frequent when more food is available. Other researchers working with the Theridiidae and the Agelenidae have found similar results, (Rypstra 1986, Krafft 1986, respectively). These findings lead me to suggest

that high food availability is a permissive factor in the evolution of sociality. In an environment without restrictive seasonality and with high food availability spiderlings may remain indefinitely at the maternal web leading to the evolution of sociality along a subsocial route.

The Dictynidae is the only family that includes cooperatively social species and does not include subsocial species. Yet it does include gregarious species (Buskirk 1981). One Dictynid species, *Amaurobius socialis*, lives in colonies that are formed by siblings building their own nests around the former maternal nest. It is very easy to imagine a scenario where groups of siblings gradually developed cooperation. Since there is no maternal care in this species, I suspect that social Dictynids have evolved along a parasocial route rather than a subsocial route.

Evolution of Subsociality

Up to this point, I have discussed the role of a subsocial species in the evolution of sociality. I will now proceed to speculate on the reasons that *T. pictum* should have evolved subsociality at all.

Many authors have described a trade-off in investment between species which have a large number of offspring and those which have a fewer number but provide them with greater parental care (Shear 1970, Smith 1982). Which strategy is used may depend on aspects of that particular species biology and/or on historical contingencies. I argue that *Theridion* species have many preadaptations which allow them to increase parental investment.

First, they may be more effective at capturing larger prey and at capturing prey

more frequently thus increasing the amount of food available at the web. While the shape and structure of the web may (or may not) simply be more efficient than other web designs, I suspect the actual technique used by comb-footed spiders is especially important. They possess 'combs' located on the tarsi of each of the fourth legs and use these to draw silk from their spinnerets and throw it over the prey. This restricts the movements of the prey while allowing the spider to avoid coming into close contact and being injured by the prey. Once the prey is partially subdued the spider closes in and quickly injects venom. Enders (1975) makes the point that the use of venom allows animals to capture relatively larger prey since it effectively increases the animals body size (as does use of a tool such as a web). In itself, capturing larger prey does not lead to greater food availability if fewer items are caught. However, if an equal volume or weight of small items versus large items were available, more spiderlings might survive given the large item since it is more difficult for one or a few individuals to monopolize the item. This is because of the high surface to volume ratio.

Second, *T. pictum's* form of web construction may increase chances of survival of the offspring. The retreat can provide important thermal insulation, as described in chapter one. It is also a place were numerous individuals can be sheltered from rain or heavy winds. Without a common retreat, spiderlings would need to find their own separate hiding places during a storm thus reducing the parents' ability to provide protection against predators or parasites. This might also lead to the loss of any group cohesion.

Third, the life cycle of any social or subsocial species must be such that an overlap of generations is possible. Obviously, in temperate climates species that overwinter as

eggs are not going to develop subsociality whereas species like *T. pictum* that overwinter as subadults and that lay their eggs in the spring are well suited to provide parental care. This may explain why the Dictynidae appear to have evolved along a parasocial rather than a subsocial route. Available information indicates Dictynids overwinter as eggs (Buskirk 1981). In fact the timing of egglaying may explain the entire dichotomy between subsocial and parasocial evolution. Thus, it would also be interesting to know whether parasocial groupings of wasps occur in species that also overwinter as eggs.

Conclusion

With the possible exception of *E. bistriata*, no orbweavers have developed cooperative forms of sociality and appear to be constrained from doing so. Instead, they have developed gregarious forms of sociality which often allow them to exploit habitats that solitary species cannot. For example, *M. gravidus* colonies are able to span small streams (Buskirk 1975). They may also benefit from being in a colony when insects rebounding off another's web get caught in their own (Lubin 1974). Sheet and tangle web weavers are more easily able to exploit the advantages of sociality by being cooperative. While it is more common for these cooperative forms of sociality to evolve along the subsocial route, parasocial evolution has probably occurred in the Dictynidae. My own research provides strong support for the hypothesis that social Theridiids have evolved from subsocial ancestors by providing a partial mechanism to explain the process.

Before drawing any conclusions regarding the causes behind the evolution of

subsociality we will need the results from comparative studies of solitary and subsocial *Theridion* species and from comparisons of other genera with *Theridion* species. In particular, greater knowledge of hunting success would be useful since I suspect that the superb prey capturing abilities of *Theridion* species is an especially important preadaptation for subsociality.

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Family	Species	Web Type	Share web supports	Share retreat	Share capture web	Share brood care	Feeds young	Lays eggs in fall or spring
Subsocial								
Theridiidae	*Theridion pictum*	Tangle	0	0	0	0	X	S
Gregarious								
Dictynidae	*Amaurobius socialis*	Tangle	X?	O	O	O	O?	S?
Araneidae	*Eriophora bistriata*	Orb	X	X	0	0	0	F
Araneidae	*Metabus gravidus*	Orb	X	0	0	X	0	Tropical
Uloboridae	*Philoponella oweni*	Orb	X	0	0	0	0	S
Cooperative								
Agelenidae	*Agelena consociata*	Sheet	X	X	X	X	X	Tropical
Dictynidae	*Mallos gregalis*	Tangle	X	X	X	X	X	F/Tropical
Eresidae	*Stegodyphus sarasinorum*	Sheet	X	X	X	X	X	Tropical
Theridiidae	*Anelosimus eximius*	Tangle	X	X	X	X	X	Tropical

Table 3.1 Social characteristics of the adults of typical species of families mentioned in the text. 0 - indicates the species does not display that trait while X indicates that it does. (Adapted from Buskirk, 1981).